

**HAPLOMITRIUM MONOICUM, A REMARKABLE NEW
SPECIES OF CALOBRYALES (HEPATICAE) FROM
NEW CALEDONIA, TOGETHER WITH A
RECLASSIFICATION OF SUBG.
HAPLOMITRIUM¹**

JOHN J. ENGEL²

ABSTRACT

Haplomitrium subg. *Haplomitrium* is circumscribed to include the following four species: *H. hookeri*, *H. ovalifolium*, *H. intermedium*, and the newly described *H. monoicum* Engel. The last possesses a combination of unique features that taxonomically isolate it. Among these are: whitish antheridia with highly abbreviated stalks that gradually merge with the antheridial body; antheridia and archegonia 1–2 per bract; the monoecious condition; bordered leaves; lack of leaf slime papillae; and the striolate-papillose cuticle. *Haplomitrium monoicum* is placed in a new section, sect. *Protohaplomitrium* Engel and is endemic to New Caledonia.

The genus *Haplomitrium* consists of some 12 species. The genus is rather widespread in distribution, but the species are, for the most part, restricted in range, as follows: *H. ovalifolium* Schust. (Campbell Is., New Zealand); *H. gibbsiae* (Steph.) Schust. [New Zealand, Tasmania (leg. Engel)]; *H. intermedium* Berrie (Australia, New South Wales); *H. blumii* (Nees) Schust. [Java, Sumatra, New Guinea, Taiwan (Inoue, 1974), Eastern Himalayas of India (Udar et al., 1968)]; *H. giganteum* (Steph.) Grolle (Philippines); *H. mnioides* (Lindb.) Schust. (Japan, Taiwan); ***Haplomitrium dentatum*** (Kumar & Udar) Engel, comb. nov. (basonym: *Calobryum dentatum* Kumar & Udar, J. Indian Bot. Soc. 55:23. 1976) plus *H. grollei* Kumar & Udar and *H. indicum* (Udar & Chandra) Schust., all from the Darjeeling region of India; *H. hookeri* [Europe, Spitzbergen, W. Greenland, Eastern North America, Western North America (Schofield, 1968; Worley, 1969), Japan (Inoue, 1971), Eastern Himalayas of India (Udar & Chandra, 1965a), Western Himalayas of India (Udar & Singh, 1977)]; *H. chilensis* Schust. (southern South America); and *H. andinum* (Spruce) Schust. (neotropics, ranging from Andean Peru and Ecuador to Lesser Antilles). Marshall R. Crosby recently collected a specimen in New Caledonia that proved to be a critical new species. This is described below.

***Haplomitrium monoicum* Engel, sp. nov.**

Planta monoica. Folia plerumque elliptica, ad apicem pro parte maxima late rotundata; margines integrae, non repandae lobatae vel dentatae. Papillae mucigeræ foliorum maturarum atque immaturarum nullae. Cellulae marginales foliorum uniseriatae, medianis grandiora et parietibus crassioribus; medianae 54–70 μm latae, 55–78 μm longae; cuticula foliorum striolato-papillosa.

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² Department of Botany, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.

Antheridia archegoniaque ad apicem axis vel prope hunc posita, 1–2 per bracteam, non in distinctum receptaculo termini aggregata. Antheridia matura eburnea, anguste ovoidea vel ellipsoidea; pedicellus 1–2 cellulae longus, crassus, a corpore antheridii vix distinctus.

TYPE: NEW CALEDONIA. Montagne des Sources Reserve, ca. 20 air-km NE of Nouméa, 750 m, 3 September 1981, Crosby 14165 (F, holotype; NOU, PC, PE, isotypes).

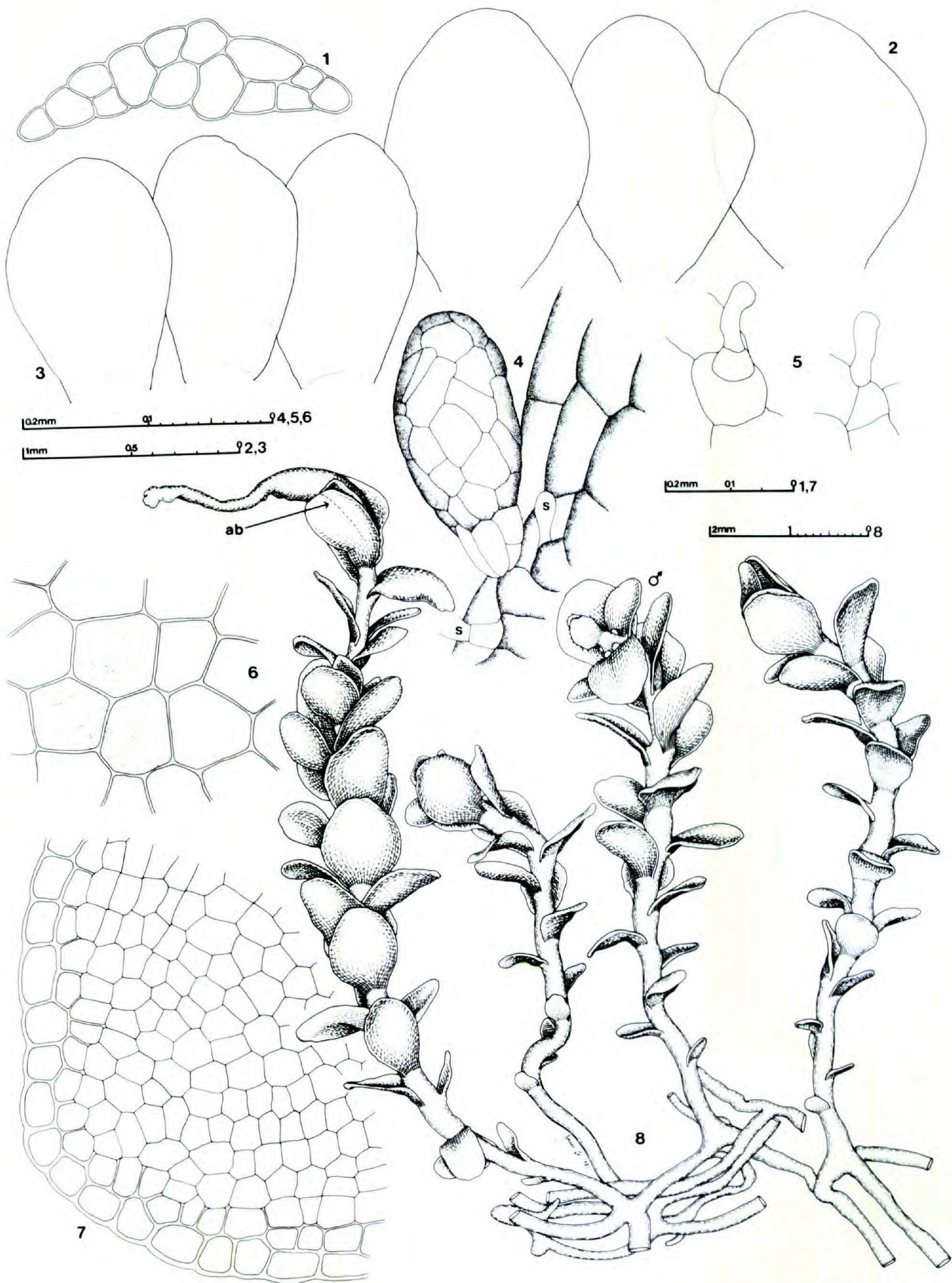
Plants fleshy, brittle, pure grass green, small, the sterile leafy shoots 1.2–1.8 mm wide, 5.4–8 mm high, isophyllous or subisophyllous and arising from a system of prostrate, pale or whitish, leafless, elongated, often ramified, basal rhizome, the rhizome sometimes gradually converted into erect, leafy axes; geotropic, leafless stolons from leaf axils and terminal furcate branching both lacking; erect shoots for most part leafy throughout, only a comparatively short, basal region naked. *Leaves* (mature) of sterile shoots subequal in size from shoot base to apex, the nodes at \pm regular intervals; leaves bistratose in a small but distinct median-basal field, the marginal 1–2 cell rows unistratose, the remainder of leaf otherwise unistratose; lateral leaves transversely to subsuccubously oriented and inserted, the dorsal leaves remaining transversely so, at least on well-developed shoots; leaf insertion often slightly acroscopically arched. Leaves erect-spreading to spreading at $\pm 90^\circ$, remote to approximate, plane or becoming gently and gradually deflexed, longer than broad, usually elliptic, less often feebly obovate or suborbicular, rather narrowed at the base; apex mostly broadly rounded, sometimes narrowly so; margins plane and not sinuous, entire. Dorsal leaves generally a little smaller and narrower than lateral leaves, the dorsal leaves at times somewhat irregular in shape, at times not perceptibly differing from lateral leaves. Leaves toward base of shoot much reduced, the proximal ones scalelike, but within ca. 2–3 leaf cycles becoming linear, then oblong prior to the mature condition. Slime papillae lacking on both leaf margins and surface. Leaves bordered by 1(–2) rows of larger cells with thicker walls than the internal ones, the marginal cells 46–55(–66) μm wide, 54–73(–78) μm long, averaging 1.1–1.7 times area of the interior adjacent cells; intramarginal cells leptodermous, large for genus, those in median portion of leaf 54–70 μm wide, 55–78 μm long; cuticle striolate–minutely papillose. *Plants monoecious*; male plants \pm same size as sterile or gynoeceal shoots, the plants not heterothallic. *Antheridia* near or at summit of shoot and not generally dispersed along axis; perigonal bracts similar to leaves; antheridia 1–2 per bract, confined to the bract axil, appearing almost sessile, whitish green ripening to ivory white (the post-dehiscence antheridia pale brown), narrowly ovoid to elliptic, with stalk 1–2 cells long, gradually grading into body, the jacket cells large; slime papillae interspersed with antheridia, the papillae either sessile or mounted on a stalk of 1 cell, the slime cell linear to elongate subclavate; antheridial terminal disc not differentiated, although the shoot apex at times becomes slightly dilated with androecial formation; swollen fertile “nodes” and subsequent apical innovation absent. *Archegonia* red brown with age, with position and number similar to antheridia: the archegonia 1–2 in or near bract axil in distal portion of axis, not confined to summit, but not becoming scattered along axis; archegonia sometimes only at axis summit, the shoot then appearing acrogynous; in other shoots, the archegonia associated with bracts below the summit, the shoots then fundamentally anacrogynous; bracts associated with archegonia

(unfertilized gynoecia) similar to leaves or smaller. *Perichaetial bracts* associated with fertilized gynoecia erect to suberect at least proximally, some becoming moderately reflexed distally, the bracts longer than wide, somewhat larger than leaves, elliptic (but more narrowly so than leaves) to oblong; accessory bracts (bractlets) often present, in unfertilized gynoecia ca. 0.3 times the leaf size and lingulate, in fertilized gynoecia ca. 0.25–0.5 the size of adjacent bracts and oblong to long-linear, inserted at base of calyptra; archegonial terminal disc not differentiated, no apical dilation of stem with archegonia formation; swollen fertile “nodes” and subsequent apical innovation absent. *Calyptra* single (rarely double) per gynoecium, translucent, long-tubular and with sides \pm parallel throughout or elongate-subclavate and gradually expanding distally, the mouth not contracted; calyptra surface smooth, the unfertilized archegonia and accessory bracts remaining at base of calyptra and not elevated upon its surface. Sporophyte not seen.

Ecology-Phytogeography.—The type was collected on a shaded, vertical, clay bank of an intermittent stream at 750 m in a stand of forest made up of *Araucaria muelleri* (emergent species here), *Strasburgeria* (in its own, monotypic family), *Zygogynum* (Winteraceae, all species on New Caledonia), *Sphenostemon*, *Canacomyrica* (monotypic genus of Myricaceae), *Nemuaron* (Monimiaceae; two species, both from New Caledonia), *Beauprea*, *Ascarina*, and *Hibbertia*. This species is known only from the type; the genus is new to the flora of New Caledonia.

Branching.—Branching in *H. monoicum* is copious, exogenous intercalary, and consists of a system of erect leafy shoots arising from prostrate, elongated, often intertwined rhizome-like axes. The rhizomes often themselves branch and remain rhizomatous, or they may occasionally gradually convert to erect, leafy axes (Fig. 8). This leafy axis either remains unbranched or gives rise to one or two rhizome-like branches from its extreme base. On very rare occasions (only one branch seen), a leafy, exogenous intercalary branch arises from a leafy axis. In this case the branch issued from the axil of a leaf about midway between the shoot apex and base, and while ascending to the height of the parent axis, was inferior in stature to it. Campbell (1959, p. 249) described such branches, which arise from an epidermal cell and lack a basal sheath, for *H. gibbsiae*. Campbell, however, described branch initiation “on the side of the stem at a point midway between two leaves of a vertical row,” and not axillary as in our plant. This branch type in *H. monoicum* is reminiscent of that shown for *H. ovalifolium* by Schuster (1971, fig. 18, right hand branch). There are, then, three possible positions of a leafy shoot, namely 1) directly from a prostrate leafless axis which continues rhizomatous growth; 2) from a rhizome, but through gradual conversion to a leafy shoot; and 3) as an exogenous intercalary branch of another leafy shoot.

The following two branch types found in *H. intermedium* are apparently not produced in our plant: 1) leafless, geotropic stolons originating from above a leaf axil; and 2) terminal, furcate branches (see Schuster, 1967, figs. VI: 1, 6). The branch system of *H. monoicum* is thus rather simplified, at least compared with that of *H. intermedium*. Branching in *H. monoicum* consists of an extensive continuous rhizome system, which at times “acts” like that of *H. gibbsiae*. In that species, “a creeping rhizome becomes ascending and leafy, and near the



FIGURES 1-8. *Haplomitrium monoicum* Engel.—1. Cross section of leaf base.—2-3. Two leaves, and between, a dorsal leaf.—4. Antheridium *in situ*, note stalked and sessile slime papillae (=s).—5. Stalked (left) and sessile slime papillae of androecia.—6. Median leaf cells, with striate-papillose cuticle indicated on some cells.—7. Distal portion of leaf showing border.—8. Habit showing monoecious condition, note antheridia (=♂).

point at which it becomes erect gives rise to a new rhizome-like axis, which again, potentially may become erect'' (Schuster, 1967, p. 35).

Attention has been placed on the knobby to spurlike, "coralloid" rhizome of *H. hookeri* which Müller (1909) illustrated and which Schuster (1967) utilized as a key character. However, the rhizome of *H. hookeri* is more variable than these authors would have it. Worley (1969, p. 228), for example, states that his material "is less 'warty' and rather freely extended throughout the substrate" Further, *Engel 17443* from Mt. Austin, Washington also has elongated nonspurred rhizomes.

Slime Papillae.—Slime papillae of *H. monoicum* occur on stem cells near the shoot apices as well as among antheridia. They may be either sessile or mounted on a cell quite wide in comparison to the slime cell (Figs. 4–5). Sessile slime papillae apparently are exceedingly rare for the family, and, in fact, Schuster (1967, p. 16) states for Calobryaceae, "Slime papillae of a single type: the stalked type." However, sessile slime papillae occur in our plant, as well as on the rhizome of *H. intermedium* (Berrie, 1962). Udar & Chandra (1965b) state that leaf slime papillae in *Haplomitrium* (= *Calobryum*) *indicum* are 1–2(–3) cells high and illustrate a sessile "mucilage papilla" (see their fig. 11).

The leaves of *H. monoicum*, even in their immature state, bear no marginal or surface slime papillae. I was unable to establish leaf slime papillae, at least on progressive stages of leaf development down to the 24- and 32-celled states. In this respect *H. monoicum* is a bit unusual, for the majority of taxa in the genus possess leaf slime papillae (also called mucilage hairs by some authors). Further, the lack of leaf papillae is of taxonomic value, for the allied *H. intermedium* indeed has them (Berrie, 1962).

Leaf Cells.—The leaves have a conspicuous border formed of a single row of cells both larger and thicker-walled than the interior cells (Fig. 7). In surface view, cells of the penultimate row exhibit three thickened walls and a thin innermost fourth wall (Fig. 7). Sporadically and locally there may be a few uniformly thickened cells forming a second row, but this is exceptional (Fig. 7, bottom right). The cells are large for the genus, being 54–70 μm wide and 55–78 μm long in the leaf middle, and thus are comparable in size to those of the non-allied *H. gibbsiae*, which has variable median cells, 40–65 \times 40–100 μm , and to *H. andinum*, with median cells 40–70 \times 65–105 μm . The cuticle of *H. monoicum* is striolate-papillose (Fig. 6); to my knowledge all other species in the genus have a smooth cuticle.

Sexuality and Gynoecia.—This is the only monoecious species known for order Calobryales (cf. Fig. 8). The archegonia, remarkably, occur in nearly the identical position and number as the antheridia. Archegonia occur only 1–2 per bract, this being the lowest number in the genus. (Also with a reduced number of archegonia is *H. intermedium*, with 4–8 per bract.) In general, the archegonia are not particularly fixed in juxtaposition to the bract, but are rather in, or in the vicinity of, the bract axil or bract base. Some shoots have archegonia solely terminal in position, although their axillary nature is still clearly demonstrable. Such shoots are acrogynous, although there is no apical swelling of the shoot and thus no suggestion of a terminal disc characteristic of subg. *Calobryum*. Other shoots possess archegonia associated with the second and third cycles of leaves

(bracts) below the axis summit. Such shoots are fundamentally anacrogynous. Prior to the work of Schuster (1967), archegonial position was used as a major criterion to separate the acrogynous condition of *Calobryum* and the anacrogynous condition of *Haplomitrium*. Schuster, however, has shown that this character is by no means as absolute as had been thought, and that the two genera in fact merge. Species like *H. intermedium* and now *H. monoicum*, which have both the acrogynous and anacrogynous conditions, are critical to this broader generic concept [which required the combination *Haplomitrium dentatum* (Kumar & Udar) Engel, made above]. Anacrogyny is almost carried to an extreme in *H. intermedium*, where we find distinct swollen archegonia-bearing "nodes" with subsequent and sometimes repeated apical proliferation of the shoot (see Schuster, 1967, fig. IV: 6). Such nodal formation appears to be restricted to that species.

Haplomitrium monoicum, like *H. intermedium*, produces accessory perichaetial bracts (or bractlets). These are inserted at the calyptra base and not elevated upon its surface.

The gynoecia nearly always produce one calyptra per gynoecium, but in rare instances there may be two well-developed calyptrae. The calyptra of *H. monoicum* is smooth throughout and does not have scales or bractlets upon its surface such as we find in, say, *H. gibbsiae*. Unfertilized archegonia remain at the base of the calyptra, and are not elevated upon its surface. This situation is similar to *H. intermedium*, *H. hookeri*, and *H. andinum* in which the calyptra is derived from the venter of the archegonium plus, at most, a limited zone of receptacular tissue beneath the unfertilized archegonia.

Androecia.—Antheridia occur at or near the shoot summit, and are not confined to definite receptacles as in subg. *Calobryum*. In this respect *H. monoicum* compares with *H. hookeri*, *H. ovalifolium* and *H. intermedium*, the last being unique in producing swollen fertile "nodes" with subsequent apical innovations.

The Crosby plant possessed both old, dehisced antheridia as well as ripe and immature, unopened individuals. The dehisced antheridia are interesting, for they are urn-shaped, with the distal half missing but the pale brown basal portion left intact, the overall appearance like that of a dehisced *Physcomitrium* moss capsule.

Schuster (1967, p. 17) states for suborder Calobryinae that "the long stalk of the mature antheridium is notable; longly stalked antheridia being exceptional in the leafy Hepaticae, except for the Schistochilaceae and Perssoniellaceae." The stalk is not only comparatively long, but quite well differentiated from the body of the antheridium; see, for example, the figures of *H. intermedium* in Schuster (1967), of *H. hookeri* in Schuster (1967) and Inoue (1971), of *H. ovalifolium* in Schuster (1971), of *H. andinum* in Fulford (1963), and of *H. blumii* in Goebel (1891, pl. 2; 1930, p. 844) and Campbell (1920).

The antheridia of *H. monoicum*, however, are unique within the family. They are narrowly ovoid to elliptic in shape, with stalks only 1–2 cells high that grade almost imperceptibly into the body of the antheridium, such that the antheridia appear almost sessile (Fig. 4). Antheridia with such abbreviated stalks and minimal differentiation of stalk and body surely must be regarded as the most primitive within the family. Highly abbreviated antheridial stalks, in fact, are rare in hepatics, and the condition in *H. monoicum* brings to mind that of the unrelated

Treubia nana (Metzgeriales), in which the stalks are two cells wide and one cell high (see Inoue, 1960). In that species, however, the stalk cells are very squat and the body is globose.

The question then arises: Is there a connection between the antheridia of our species and the type prevalent in the remainder of species in *Haplomitrium*? The stalk of *H. gibbsiae* appears to be relatively short. According to Campbell (1959), the stalk of the mature antheridium of that species is 3–5 tiers of cells in height. Moreover, the figures of this species in Schuster (1967) are particularly revealing, for the stalks expand somewhat gradually toward the body. Thus, features of the stalk (cell number and stalk form) in *H. gibbsiae* somewhat approach those of *H. monoicum*.

Relationships.—*Haplomitrium monoicum* belongs to a well-defined ensemble of species that constitutes subgenus *Haplomitrium*. These taxa are *H. monoicum*, *H. intermedium*, *H. ovalifolium*³, and *H. hookeri*, and are characterized by 1) archegonia and antheridia at least in part scattered and indefinite in position and not consistently confined to terminal receptacles, the archegonial shoots at least in some cases thus anacrogynous; 2) shoots at least potentially indeterminate in growth and leafy throughout their length, bearing a number of cycles of mature leaves; 3) leaves of sterile shoots subequal in size throughout axis, usually longer than wide and either unistratose throughout or with a limited field of polystraty at extreme base; and 4) antheridia yellow to pale orange (except *H. monoicum*).

The nearest, but not particularly close, relative of *H. monoicum* is *H. intermedium* of Australia. The two taxa share such features as 1) large leaf cells, being 54–70 μm wide and 55–80 μm long; 2) general elliptic leaf shape, although *H. intermedium* varies toward an ovate outline; 3) accessory perichaetial bracts or bractlets; and 4) small plant size.

Haplomitrium monoicum is noticeably distinct from *H. intermedium*, differing from that species in 1) the bordered leaves; 2) the completely entire leaves, which do not develop slime papillae, even on very young leaves; 3) the broadly rounded leaf apices; 4) the bistratose leaf base; 5) the striolate-papillose leaf cuticle; 6) the nonpigmented antheridia with stalks only 1–2 cells high, and with stalk and body gradually merging; 7) the lack of stolons and terminal branches; 8) the reduced number of archegonia per bract; and 9) the monoecious condition. The magnitude of these differences, together with the number of unspecialized features—namely 2), 6), 7) and 8) above—speak for a very unspecialized species which belongs in a section of its own, as follows:

Haplomitrium sect. **Protohaplomitrium** Engel, sect. nov.

Planta monoica, rhizomatibus basalibus et erectis axibus foliosis solum instructa; stolones et rami terminales nulli. Cellulae marginales foliorum uniseriatae, medianis grandiora et parietibus crassioribus; cuticula foliorum striolato-papillosa; papillae mucigerae foliorum maturarum atque immaturarum nullae. Antheridia archegoniaeque ad apicem axis vel prope hunc posita, 1–2 per bracteam, non in

³ Since *H. ovalifolium* is known with sparing gynoecial plants, the anacrogyny of this species has not been firmly established. However, Schuster (1971, p. 139) states that "isolated archegonia occasionally [are] present in the axils of subfloral bracts." Further, the vegetative plants and scattered antheridia closely match those in subg. *Haplomitrium*, and I do not hesitate to place it there.

distinctum receptaculo termini aggregata. Antheridia matura eburnea, anguste ovoidea vel ellipsoidea; pedicellus 1–2 cellulae longus, crassus, a corpore antheridii vix distinctus.

TYPE: *Haplomitrium monoicum* Engel.

With the discovery of *H. monoicum* and *H. ovalifolium* (Schuster, 1971), there has been a reduction in degree of isolation of the monotypic subgenus *Archibryum* that Schuster (1967) had established for *H. intermedium*. I would prefer a sectional level for that species, as follows:

Haplomitrium sect. *Archibryum* (Schust.) Engel, stat. nov. Basionym: *Haplomitrium* subg. *Archibryum* Schust. Nova Hedwigia 13:28. 1967.

The taxa of subgenus *Haplomitrium* may be separated by the following key:

KEY TO TAXA OF *HAPLOMITRIUM* SUBG. *HAPLOMITRIUM*

- 1a. Leaves with a conspicuous border of large thick-walled cells, the interior cells smaller and leptodermous; leaf apices mostly broadly rounded; leaf margins completely entire, not repand, without tendency toward lateral teeth or lobes; leaf slime papillae lacking, even on young leaves; cuticle striolate-papillose; antheridia ivory white, the stalks 1–2 cells high, gradually and almost imperceptibly grading into body; plants monoecious. New Caledonia. Sect. *Protohaplomitrium* *H. monoicum*
- 1b. Leaves without a border; leaf apices variable, ranging from narrowly rounded to blunt to blunt pointed; leaf margins often repand to repand-lobate, sometimes with teeth or lobes; leaf slime papillae present, at least on young leaves (? *H. ovalifolium*); cuticle smooth; antheridia yellow to light orange, the stalk and body clearly differentiated and not gradually merging, subequal in length; plants dioecious 2.
- 2a. Leaf cells large, 40–50 μm wide, 55–80 μm long; branching complex: besides upright leafy shoots and basal rhizomatous axes the plants developing 1) leafless, geotropic stolons originating from above a leaf axil, and 2) terminal furcate branches; androecial shoots with conspicuous, swollen fertile "nodes" with subsequent, sometimes repeated, apical proliferation of the shoot; leaves unistratose throughout. Australia. Sect. *Archibryum* *H. intermedium*
- 2b. Leaf cells small, 24–45 μm wide, 25–55 μm long; branching simple: besides upright leafy axes and basal rhizomatous axes, the plants developing only exogenous intercalary branches of leafy shoots, the plants without stolons or terminal branches; androecial shoots of \pm the same width throughout, without swollen "nodes"; leaves with a small, basal, at least bistratose field, the leaves otherwise unistratose. Sect. *Haplomitrium* 3.
- 3a. Leaves never bifid, often diamond shaped to ovate-triangular, mostly with a low terminal lobe and 2 obtuse lateral lobes, the leaves sometimes wider than long; oil-bodies usually homogenous. Northern Hemisphere *H. hookeri*
- 3b. Leaves sometimes bifid to base, mostly ovate to ovate-lanceolate, the margins at most obscurely repand to repand dentate, not lobed, the leaves always longer than broad; oil-bodies \pm clearly botryoidal. New Zealand, Campbell Island *H. ovalifolium*

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